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The worst thing that can be said of Jonathan Birch's *The Philosophy of Social Evolution* is that the title of the work doesn't even hint at the breadth and wealth of material hidden within. Birch's style is understated throughout and he is careful to give a fair and respectful hearing to all the ideas and thinkers he discusses. In so doing, he systematically develops a comprehensive and novel framework for understanding social evolution, in all its forms. It is possible to read *The Philosophy of Social Evolution* as an extended essay on the importance and application on three related insights from the great biologist W.D. (Bill) Hamilton: Hamilton's Rule, kin selection, and inclusive fitness. Indeed, Birch describes his book as "one long argument for the

cogency and explanatory power of Hamilton's ideas" (10). Hamilton's ideas are the foundation from which Birch's larger theory of social evolution springs.

Hamilton's rule is one of the most foundational of these ideas in evolutionary theory and Birch devotes substantial attention to it. Hamilton's rule states simply that nature can select for a particular strategy when the product of the relatedness of the members of the population with that strategy and the benefit of the strategy are greater than the fitness cost of the strategy. Put in its usual form, the rule is expressed as $rb > c$ where r is the relatedness coefficient (typically between 0 and 1), b is the benefit to fitness of the strategy, and c is the fitness cost of the strategy. As Birch puts it, "the rules tell us that the gene for a strategy are favoured when the cost to the actor is offset by a sufficient benefit to sufficiently related recipients" (37).

Hamilton's rule is central to models of the development of altruism since Hamilton shows how a costly strategy like altruism might be able to evolve. If the cost of a strategy is greater than zero but the product of the relatedness coefficient and the benefit of the strategy is high enough, costly traits like altruism can evolve. Indeed, Hamilton provides a general schema for social behavior based on whether an actor, whose strategy has an effect on some recipient create a net cost or benefit through interaction.

		Recipient	
		Benefit	**Cost**
Actor	**Benefit**	Mutual Benefit	Selfishness
	Cost	Altruism	Spite

Table 1—Hamilton's Schema

Altruism's evil twin is spite, which is costly to both parties and beneficial to neither. The evolution of mutually beneficial and selfish strategies, which both accord benefits directly to the actor, are easy to explain. Altruism and spite, however, are more mysterious since the benefit is lower than the cost and, hence, for altruism to evolve relatedness needs to be high. For spite to evolve, relatedness needs to be negative (the product of a negative benefit and negative coefficient of relatedness is positive). Hamilton's rule can explain, in principle, the evolution of all these strategies.

Despite its theoretical power, Hamilton's rule has its critics. Recently, Martin Nowak, Corina Tarnita and E.O. Wilson published what Birch calls a "strongly worded" (37) article in *Nature* arguing that Hamilton's rule cannot explain the evolution of sociality since the model lacks external validity. Group selection rather than the kin selection predicted by Hamilton's rule, they argue, is a likelier candidate to explain the evolution of sociality. This article kicked off a heated debate in the pages of *Nature* and elsewhere about the assumption required for Hamilton's rule to explain the evolution of altruism. Birch spends Chapter 2 and 3 defending of Hamilton's rule in the face of these criticisms.

His argument relies on extending work by David Queller showing that Hamilton's rule can be represented as a population level model by modifying it to allow for "polygenic traits" (40-41). Among other things, this derivation assumes that $E(w_i \Delta p_i) = 0$, i.e. that there are no effects from drift and migration (44). Birch shows in Chapter 2 and the Appendix how the Price equation can be modified sufficiently to represent Hamilton's rule as a population model of the

average change in a trait. Birch, following Queller, calls this version of Hamilton's rule 'HRG,' a 'general' variant of Hamilton's rule (44).

$$\text{HRG: } \Delta\bar{p} > 0 \leftrightarrow rb > c, \text{provided } \mathrm{Var}(p_i) \neq 0$$

This model, Birch argues, provides a general framework for analyzing the evolution of traits since the coefficients in the HRG are "properties of populations, not of individual organisms or token social interactions" the meaning of 'relatedness,' 'cost,' and 'benefit' can be applied more broadly in meaningful and explanatory ways (45). As Birch notes, once we think about the elements of Hamilton's Rule at the population level, $rb > c$ is all about the relative difference, that is, "c and b quantify the *differential* fitness effects of having higher than average value…and r quantifies the *differential* genetic similarity" (45). This explains how the Hamilton's rule can apply even when the values are negative and, hence, how spite and altruism can evolve through the same mechanism of indirect fitness.

There is much more to say about HRG and Birch spends considerable space on explaining it as well as defending various aspects of it against potential criticisms. The general point, though is that Nowak and Wilson are wrong to think that Hamilton's Rule is either trivial or false and that it cannot explain the development of sociality. If we understand Hamilton's Rule in the way that Birch argues we should, "HRG organizes social evolution research by allowing us to locate specific modelling results in the space of explanations" (50). In particular, HRG allows us to distinguish between traits that are indirectly fitness enhancing ($rb \geq c$ and $c \geq 0$), directly fitness enhancing ($rb \leq c$ and $c \leq 0$), some hybrid of the two ($rb \geq c$ and $c \leq 0$), or does not

admit of a fitness-based explanation. This interpretation of HRG as a fundamental organizing framework is crucial to the rest of the work.

The middle of the book is devoted to thinking through how one of Hamilton's other key ideas, kin selection, is different from or connected with the resurgent ideas of group selection. The answer lies in the idea of relatedness and in the importance of structure in populations. There is much to say about the importance of the arguments in this part of the book and the discussion of kin and group selection is especially important to clarifying some of the most heated debates currently raging in biology, but it is the final sections of the book that I want to focus on in the rest of this review.

Beginning in Chapter 7, Birch begins moving from abstract models of social evolution to more specific application in social life. Using the techniques that he developed earlier in the book, Birch argues that the 19th century idea of the "cell state," i.e. the organism as an economy of interacting cells. This framework fits in well, Birch argues, to the "major transitions" approach in biology. Organisms provide environments for positive feedback in what amount to economies of scale. Larger organization structure in organisms allow for positive returns to scale because they allow for "functional versatility" (specialization) and, more importantly, "redundancy," which is important for the robustness.

The insight here is a profound one and, if anything, Birch undersells its importance. The only Smith mentioned in the text is John Maynard, but the idea that Birch develops in the context of the economy of the organism is exactly the same one that Adam Smith came to about the

economy generally in *The Wealth of Nations.* There Adam Smith argues that the division of labor is limited by the extent of the market. What he meant is that there are both gains to trade through specialization and increasing returns from scale and specialization. These are roughly the same reasons that Birch gives for his argument in favor of "increasing returns" to scale in organisms. Neither Smith nor Birch (183) claims that these increasing returns can continue indefinitely and there are important questions about how to measure and understand positive feedback from scale in organisms and economies, but Birch's analysis not only advances our understanding of biological organization, it also suggests an important link between economics and biology that may bear valuable analytic fruit in further research.

In the final Chapter, Birch develops what he calls the "cultural relatedness hypothesis." In broad strokes, the idea here is that cultural rather than biological closeness can connect individuals into groups that extend far beyond their closely related bands. This allows for a form of cultural selection that differs from cultural selection based purely on biological fitness. Birch conjectures that "in the Holocene…institutions such as religions and professions have allowed cultural fitness to become almost entirely decoupled from biological fitness" (201). The idea is that a religious leader, e.g. Jesus or Paul, who had no direct biological descendants can, nevertheless, have many followers who carry on their ideas and cultural norms. We can make this idea more precise by deriving a cultural version of the Price equation and, hence, "a cultural analogue of Hamilton's Rule" (202). The details of this take up most of Chapter 8, but if Birch is right, his approach provides a cultural selection model that doesn't require the strong and somewhat questionable assumptions about the size and structure of early human bands of what Birch calls

the “cultural group selection” approach of Robert Boyd and Peter Richerson or direct appeals to group selection.

I have only been able to give a cursory overview of this unusually dense and provocative book. Birch is extremely clear and careful in the development of his ideas and this makes the breadth and depth of this work even more impressive. *The Philosophy of Social Evolution* will, I suspect, become required reading in several different fields and, as I have suggested, there are insights here that extend beyond the philosophy of biology and evolutionary theory.